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NUMBER 4
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THE HUMAN BRAIN EVOLVING:

Paleoneurological Studies in Honor of Ralph L. Holloway

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FRONT COVER CAPTIONS

Center: Portrait of Ralph L. Holloway.
Upper left: A modern human brain.
Upper right: Ralph measuring landmarks on an endocast ca. 1976.
Lower right: Homo habilis cranium KNM-ER-1813 from Koobi Fora, Kenya (photo by Holloway).
Lower left: Ralph with an endocast of the Flores "hobbit" cranium.

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CHAPTER 17

MOSAIC COGNITIVE EVOLUTION: THE CASE OF IMITATION LEARNING

FRANCYS SUBIAUL

INTRODUCTION

Among Ralph Holloway's many contributions to anthropology is the notion of mosaic brain evolution; Specifically, the notion that the human brain is more than just a larger primate brain or an expanded rodent brain. Support for this view comes from research on hominid endocasts, the only direct evidence of human brain evolution available, showing that hominid brains underwent a number of organizational changes including prominent changes to visual striate cortex and the parietal lobe (Holloway, 1996) as well as the temporal lobe (Rilling & Seligman, 2002). These changes—produced by evolutionary forces—led to changes in overall size as well as regional changes in volume, hemispheric asymmetry, the distribution of fiber track connections within and between hemispheres, and species-specific variation in neuro-receptor distributions (Holloway, Broadfield, Yuan, 2004).

In 1967 Holloway hypothesized that this pattern of mosaic brain evolution resulted from selection for "complexity management." By complexity management Holloway (1967) referred to a subset of continuous primate behavioral traits "related to the efficiency and fineness of discrimination, and adaptive problem-solving ability, which includes factors such as memory storage [encoding], recall, attention-span, and delay responses" (5). These basic processes contribute to multiple psychological systems as such they represent 'domain-general' cognitive processes. Selection for specific behaviors likely favored a number of neural changes that affected how these domaingeneral processes contributed input to domain-specific mechanisms. That is, mechanisms that solve specific adaptive problems such as theory of mind or the causal properties associated with tool-use. Here I hope to build on some of Holloway's (1967) ideas, specifically, the notion of mosaic brain evolution and the forces that produced such, and further explore Holloway's ideas concerning how selection acted indirectly on the brain through it's selection of the specific actions and behaviors it produced given that behavior is what selection ultimately acts upon (Holloway, 1979; 1981; 1996). As such, mosaic brain evolution is necessarily a reflection of mosaic cognitive evolution at both general (i.e., memory and attention) and specific (i.e., tool-use and language) levels. The notion of mosaic brain evolution contrasts with both domain-general views of intelligence, such as those that propose a conceptual 'g' or general intelligence (Jensen, 2000) or pan selectionist theories such as the Social Intelligence Hypothesis (Jolly, 1966; Humphrey, 1976; Byrne & Whiten, 1990; Whiten & Byrne, 1997) or the Ecological Intelligence Hypothesis (Parker & Gibson, 1977; Parker & McKinney, 1990) and most resembles the view of cognition proposed by Evolutionary Psychology (Buss, 2006; Tooby & Cosmides, 1990).

Here I will focus on the nature and evolution of the imitation faculty; a psychological faculty that has typically been regarded as an all-purpose learning mechanism (Buller, 2006); a type of 'general intelligence,' the product of selection for 'social intelligence.' To the contrary, imitation appears to be a mosaic cognitive faculty whose evolution was not the result of a general selective force favoring social or technical intelligence, but rather its evolution is the product of a confluence of factors some that are 'social' others that are 'ecological' and still others that are 'technical.' These different pressures from these different domains produced different imitation mechanisms, specialized in the imitation of different rules and responses. As a result, our species' seemingly domain-general imitation skill is something of an illusion. It is an illusion because our ability to imitate different types of information results from the operations of many different imitation mechanisms that give the appearance of a 'general purpose' psychological faculty. Such an imitation faculty was likely to be very useful for solving a number of problems. Some of these problems include: (a) the problem of learning dominance relationships, where individual can minimize injury by inferring from observational learning who is likely to be dominant/submissive, (b) the diet problem; learning what is edible and what isn't or the problem of what to eat when, (c) the problem of alliances and cooperation, where individuals can minimize the risks of bad alliances by inferring from observation who is a reliable/unreliable partner, (d) the problem of extractive foraging, where individual can learn from others how to process or acquire protected food products, (e) the problem of social convention, where individuals use others' behaviors to guide where and when they should display species-typical behaviors or behavioral traditions. And, there are certainly others. In each instance, specialized mechanisms in the imitation faculty in coordination with other cognitive faculties grant individuals the flexibility to make rapid inferences about the dispositions of others or the causal structure of actions, bypassing the costs associated with trial and error learning, which in some instances may be lethal (e.g., the diet problem). Some of these instances require 'imitation learning' or novel imitation (when knowledge is first acquired and reproduced) but others only require the copying of species-typical behaviors—familiar imitation (e.g., social conventions)—where previously acquired behaviors (either by imitation or trial and error) are appropriately and adaptively displayed.

The Multiple Imitation Hypothesis' (Subiaul 2007) distinction between different imitation mechanisms may explain many of the similarities and differences reported between human and ape imitation performance. The argument that will be put forth in this essay is that humans and apes share some but do not share all imitation mechanisms. Differences in the number and type of imitation mechanisms available to individual species likely rests on the unique adaptations that resulted from different species-specific problems encountered in the species' environment of evolutionary adaptedness (Buss, 2007; Tooby & Cosmides, 1990) and the consequences of how selection favored different strategies for complexity management in different ape lineages (Holloway, 1967).

THE MANY FACES OF IMITATION

The Multiple Imitation Hypothesis

Most view the imitation faculty as a domain- and content-general mechanism that operates across different problem domains and content types, allowing individuals to learn everything from motor rules such as how to use chop sticks, to vocal rules such as *aguacate* ('avocado' in Spanish), to procedural rules such as how to cook your favorite pasta dish. Given what is known about the imitation skills of human children and other primates, it appears that the environment of early hominids favored individuals who were flexible imitators, capable of copying a wide range of behaviors and responses: from using chop sticks, among other tools, to saying *aguacate*, among other novel sounds, to cooking pasta among other procedural rules. However, the representation of auditory stimuli (such as *aguacate*) for the purposes of reproducing that sound must be fundamentally different than the representation of a motor action (such as using chop sticks) for the purposes of copying that action. A general-purpose mechanism capable of performing these different tasks seems unlikely if not improbable. What is more likely is that selection sifted through individuals with varying imitation skills and a unique cognitive-neural imitation profile capable of identifying, representing and copying these different types of information. This process would have produced distinct imitation skills mediated by specific imitation mechanisms dedicated to representing and copying specific types of stimuli. From this it follows that humans are good imitators relative to other primates not because we have an imitation mechanism that primates lack but because our species has evolved a whole suite of distinct imitation mechanisms or 'imitation instincts' that together result in an impressive ability to copy all sorts of responses in a flexible and adaptive fashion.

This view of imitation fundamentally differs from the widely held domain-and content-general view of imitation. The multiple imitation hypothesis proposes that the imitation faculty is similar to other vertical cognitive faculties (Fodor, 1983), such as language, that are modular, specialized and consist of multiple components with discrete functions. However, it's unlikely that the imitation faculty is as encapsulated as Fodor (1983) proposed for visual systems, for example (c.f., Marr, 1982). In this conceptualization, the imitation faculty represents a specialized psychological mechanism with input from a number of domain-general systems like memory and attention as well as domain-specific 'core knowledges' that include 'theory of mind,' 'naïve physics' and 'naïve biology' (Spelke, 2000). Through this kind of domainspecificity, the imitation faculty can copy responses across different domains in a flexible and adaptive fashion.

Like other faculties, the imitation faculty can be divided by its various functions. These functions are best captured by super-ordinate and sub-ordinate imitation mechanisms associated with the processing of specific types of stimuli (e.g., novel, familiar, auditory, motor, social, etc.). The super-ordinate imitation mechanisms include, (a) 'familiar imitation,' or the copying of familiar rules or responses and (b) 'novel imitation,' or the copying of novel rules or responses; often referred to as 'imitation learning,' which is distinguished from 'familiar imitation' in that it requires observational learning. That is, the ability to learn through vicarious (rather than direct) reinforcement (Bandura, 1977). Various researchers have made similar class distinctions, recognizing that different mechanisms likely mediate the learning and copying of a novel behavior(s) and the copying of behaviors that already exist in an individual's repertoire (Byrne & Russon, 1998; Heyes, 2001; Visalberghi & Fragaszy, 2002). However, these investigators have tended to argue that these skills are not related and consequently have tended to give these skills different names, which imply that they exist outside of a dedicated cognitive faculty for imitation. The reason for this being that many of these researchers believe that imitation is a single unitary cognitive process that animals either have or lack entirely (e.g., Tomasello & Call, 1997). In this framework, familiar and novel imitation mechanisms are brought together as part of the same cognitive faculty that mediates the ability to flexibly copy rules or responses across contexts. Moreover, subsumed within those two broad functional concepts are sub-ordinate mechanisms of imitation that specify the type of stimuli that is reproduced by either novel or familiar imitation (i.e., auditory, motor, cognitive).

As has been noted, all the proposed imitation mechanisms are characterized by flexibility *and* specificity. The flexibility requirement means that the behavioral rule that is copied is deliberate or replicable. That is, can be elicited in multiple contexts on multiple occasions; not the result of happenstance or trial and error learning or the product of narrow contextual cues. The specificity requirement emphasizes that individuals must copy a specific 'rule.' The term 'rule' is broadly defined as a response involving more than two steps (e.g., with a distinct 'beginning-middle-end' structure) that are hierarchically organized and structured to achieve a matching response. The requirement that any type of imitation be rule-governed and flexible is necessary in order to differentiate imitation from either perceptual or motivational mechanism that in association with rapid trial-and-error learning may represent an ancestral learning mechanism that predates (and may, perhaps, co-exist) with the imitation faculty, providing critical input to the mechanism mediating familiar imitation, for example. The same is true of narrow species-specific skills such as copying mate preferences that while impressive, learning does not extend beyond a very narrow context (i.e., mating) and is dependent on specific stimuli (i.e., females) (Bshary & Grutter, 2006; Paz y Miño et al., 2004). Nevertheless, such studies provide important evolutionary clues into the origins of the imitation faculty; highlighting for instance, how selection for multiple content-specific observational learning skills could be aggregated by natural selection resulting in an imitation faculty like the one described here.

Super-ordinate mechanisms of imitation: Novel imitation

Part of the confusion in the imitation literature is that 'imitation' has been largely conceptualized as 'novel imitation' or the imitation of novel behaviors. For example, in 1898, Thorndike defined imitation as "learning to do an act from seeing it done" (p. 79). Nearly a half-century later, Thorpe defined imitation more narrowly and in purely behavioral terms: "copying a novel or otherwise improbable act" (p. 122). These definitions are often viewed as synonymous, but they are quite different. One core difference between these two definitions is the requirement that individuals *copy* another's behavior. Copying is, arguably, the essence of imitation. After all, what is imitation if it isn't copying something? Yet, Thorndike's definition doesn't mention or imply copying but rather observational learning. The distinction between observational learning and imitation is critical. It is possible to learn something from another, yet not overtly express the acquired knowledge; for example, learning what *not* to do. In such instances, one can learn from a model without imitating the model. Thorpe's definition, unlike Thorndike's, stresses both (observational) learning and copying. Learning is implied in the criteria that what is copied is 'novel' rather than something that already exists in the observer's behavioral or cognitive repertoire. Despite a number of qualifications and revisions (e.g., Galef, 1988; Tomasello & Call, 1997; Whiten & Ham, 1992), Thorndike (1898; 1911) and Thorpe's (1956) definition of imitation remain influential because of their simplicity and the ease with which they lend themselves to experimentation. Nevertheless, these definitions, which conceptualize imitation as the copying of specific and novel motor responses, have largely ignored an equally important function of the imitation faculty, familiar imitation.

Super-ordinate mechanisms of imitation: familiar imitation

Familiar imitation involves the ability to flexibly and adaptively copy common or recognizable rules/responses that exist within an individual's behavioral repertoire. In the motor domain, everyday actions fall into two distinct and conceptually significant categories: transparent versus opaque. Transparent responses are those responses that are immediately available to the senses such as transitive actions that involve reaching for and interacting with objects and, as a result, may be executed via a visualvisual match (i.e., my hand on an object looks like your hand on an object). However, opaque responses cannot be executed in the same fashion, as they are not available to the senses in the same way as transparent actions. Consider the act of imitating someone scratching their head. What you perceive when you see someone scratch their head is very different from what you perceive when you scratch your own head. The phenomenological experiences are very different. This problem of translating a visual experience into a corresponding proprioceptive response has been termed the "correspondence problem" (Dautenhahn & Nehaniv, 2002).

While to some, the distinction between 'novel' and 'familiar' imitation may be obvious, there is significant debate as to what should count as a 'novel' response. Does 'novel' imply an entirely new behavior? By the most strict of standards this would exclude all species-typical behaviors; a constraint that significantly limits research questions. One way around such a constraint is to require animals to execute a series of familiar behaviors in arrangements that are never (or rarely) observed. This technique—of stringing familiar actions in an arbitrary sequence—has been employed by a number of animal researchers (apes: Whiten, 1998; birds: Nguyen et al., 2005; monkeys: Caldwell & Whiten, 2002) and represents one way of operationalizing 'novelty' in imitation research. Another technique has been to use a tool in novel problem-solving tasks (e.g., Visalberghi & Fragaszy, 1989, 1990, 1995; Whiten & Horner, 2007). Perhaps these studies, more than any others, represent the most strict standards of novelty, as subjects must often learn how to handle the tool and then learn how to use the tool *in relation* to another object. However, this poses a unique problem when comparing human and non-human ape imitation studies that involve tool-use because humans may have unique causal conceptual mechanisms and by extension, species-specific skills pertaining to objects in general and tools in particular that nonhuman primates may lack (Johnson-Frey, 2003; Povinelli, 2000). But there are other ways to operationalize 'novelty' without using tools or specific motor responses. Subiaul and colleagues (2004), for instance, developed a cognitive imitation paradigm, where subjects had to copy novel serial rules independently of copying novel motor actions. All of these tasks require that subjects learn something new in order to be reinforced, and exclude the possibility that subjects already know how to execute the target response. At the same time, such tasks control for the possibility that the ability to execute the motor response interferes with expression of knowledge gained during observation.

Others have tried to operationalize 'novelty' using single and familiar actions on objects (e.g., Apes: Hopper et al., 2008; Monkeys: Bugnyar & Huber, 1997; Voekl & Huber, 2000; 2007). Here, the rationale is that while a behavior such as mouthing is species-typical, mouthing an object in order to open it is novel. The problem is that animals often explore objects using their mouths and certainly use their mouths on objects associated with food. So, while a particular behavior directed toward a specific object may be unique, the actual behavior is not. In this regard, it's more likely that familiar imitation of the familiar action (e.g., mouthing) rather than novel imitation is the primary mechanism underlying the behavioral response in single-action paradigms. Such paradigms also make it difficult to distinguish between various mechanisms of the imitation faculty and the products of perceptual and motivational mechanisms in which, for example, an animal's interaction with an object may direct an observer's attention to that object (stimulus enhancement) or a part of that object (local enhancement), motivating the observer to interact with it (social enhancement). In such instances, these two individual's responses may be very similar, yet the similarities are likely to be the products of stimulus and social enhancement as well as rapid trial-and-error learning, rather than by any mechanisms of the imitation faculty.

Sub-ordinate mechanisms of imitation: cognitive, motor & vocal imitation

In addition to distinguishing between familiar and novel imitation, it is important to distinguish between various sub-ordinate mechanisms that form part of the imitation faculty. These mechanisms involve copying different classes of stimuli, for example, auditory, motor, and cognitive stimuli. The reproduction of these different types of stimuli compromise three particular classes of imitation: vocal imitation (the imitation of vocal/auditory responses), motor imitation (the imitation of motor actions), and cognitive imitation (the imitation of cognitive rules, including rules governing serial order, social conventions and spatial relationships, for example). The distinction between superordinate mechanisms of imitation (e.g., novel v. familiar) and sub-ordinate mechanisms of imitation (e.g., vocal, motor and cognitive) are important because it allows researchers to specify what type of imitation they are capable of. For example, an individual may be able to reproduce *familiar* vocal rules (e.g., words), but may not be able to copy *novel* vocal rules (e.g., novel words). Moreover, individuals may be able to copy novel *cognitive* rules (e.g., serial order), but not novel *motor* rules (e.g., specific action sequence). Some of these dissociations appear to be true in monkeys for instance, which seem unable to copying novel motor rules, but can copy novel cognitive rules (Subiaul et al., 2004; 2007). Interestingly, similar dissociations exist within humans. For example, children with autism, are unable to copy novel motor rules, but can copy familiar motor rules (Williams, Whiten & Singh, 2004). There's also a dissociation in novel imitation performance among individuals with autism that parallels the dissociation in monkeys; in particular a dissociation between novel motor and novel cognitive imitation (Subiaul, Lurie, Romansky, Cantlon, Terrace, 2007).

This framework does not necessarily challenge familiar terms that have become an integral part of the imitation literature such as emulation—where individuals copy the outcomes or 'affordances' of actions—or goal emulation—where individuals copy the 'intended' action of others using idiosyncratic means. Rather, it questions the logic that terms such as emulation are alternatives to imitation or more precisely, that 'emulation' is a mechanism that exists outside the mechanisms of the imitation faculty as described here. Rather, I advance the contrarian's view that terms such as emulation and goal emulation describe the imitation of different types of rules or responses; specifically, copying rules—novel or familiar—about environmental affordances or goals, respectively.

Neurobiology of familiar and novel imitation

Recently, a number of advances have supported the multiple imitation hypothesis (Subiaul, 2007). A functional dissociation between novel and motor imitation is supported by neuropsychological and neurophysiological research. In a series of studies, Rumiati and Tesari (2002, 2003) presented two groups of subjects with two different tasks: one involved copying familiar "meaningful" actions; the other involved copying novel "meaningless" actions. Meaningful (i.e., familiar) actions consisted of common actions such as brushing one's teeth. Meaningless actions (i.e., novel, arbitrary actions)[1] consisted of performing common actions in an arbitrary fashion, for example, a brushing action performed with the right arm extended outwards and the hand held upright. Predictably, subjects copied "meaningful" actions with fewer errors than meaningless actions. Rumiati and Tesari interpreted these results to mean that different systems mediate the imitation of "meaningful" and "meaningless" actions. In their model, the perception of familiar actions are recalled from long-term memory then moved into working-short-term memory in order to generate a matching motor output. The perception of novel "meaningless" actions, however, is processed in working-shortterm memory as there's no memory trace to recall from semantic long-term memory.

Neuroimaging studies conducted by the authors have provided additional support for a dual-processing route. Rumiati, Weiss, Tessari and colleagues (2005), reported that the left inferior temporal gyrus was associated with a significant increase in blood flow when subjects copied meaningful actions. Whereas, greater blood flow to the parieto-occipital junction was associated with copying meaningless actions. When comparing neural activation during the imitation of familiar relative to unfamiliar actions there were differential increases in neural activity in the left inferior temporal gyrus, the left parahippocampal gyrus, and the left angular gyrus, structures associated with longterm memory processes. Whereas, the superior parietal cortex (bilaterally), the right parieto-occipital junction, the right occipital–temporal junction (MT, V5), and the left superior temporal gyrus where differentially active when subjects copied novel actions relative to familiar actions. The primary sensorimotor cortex, the supplementary motor area, and the ventral premotor cortex showed increased neural activity when subjects copied both types of actions (familiar and novel).

There are a number of studies that are consistent with the multiple imitation hypothesis (Buccino et al., 2001; Cochin et al., 1999; Fadiga et al., 1995; Decety & Chaminade, 2005; Heyes, 2002; 2005; Stevens, Fonlupt, Shiffrar & Decety, 2000). For instance, various neurophysiological studies using transcranial magnetic stimulation (TMS), magnetoencephoalography (MEG), positron emission tomography (PET), and functional magnetic resonance imaging (fMRI) have found that when subjects observe an individual executing an action using a specific muscle group, corresponding areas of the observer's motor strip is activated, as if the observer was executing the action themselves rather than passively observing someone else performing the same action (Buccino et al., 2001; Cochin et al., 1999; Fadiga et al., 1995). Consequently, when one sees a conspecific execute actions that are familiar and form a part of one's own motor repertoire, neural regions such as the supplementary motor area (SMA), the premotor cortex, and the superior and inferior parietal cortices—the action preparation system—are activated. This "motor resonance" phenomenon is not triggered by novel actions because they are not present in the motor repertoire of an observer and are yet to be learned. When individuals observe novel actions they have no existing representations of the motor component of these actions. At best, they can call upon related or similar rules or responses. As implicated by the dual-route model (Rumiati & Tessari, 2002; 2003; Tessari & Rumiati, 2004), the match between what is seen and what is ultimately executed must be done online (in working memory) with little or no help from existing cognitive representations of the target action.

The apparent motion paradigm (Shiffrar and Freyd, 1990) has further highlighted the functional and structural differences associated with copying novel as opposed to familiar actions. Using PET technology, Stevens et al (2000) presented participants with a human model engaged in possible (i.e., familiar) and impossible (i.e., novel) biomechanical paths of apparent motion. When the subjects perceived 'possible' paths of human movement, the left primary motor cortex and the parietal lobule in both hemispheres were found to be selectively activated. These areas were not activated when participants observed impossible biomechanical movement paths.

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[1] It's important to point out, however, that novel actions could be perceived as meaningful, yet, not exist in the observer's behavioral reportoire. For example, we may observe two American Sign Language (ASL) speakers communicate with one another. Though the actions are novel to us because we are unfamiliar with ASL, the signs are, nevertheless, recognized as being "meaningful." That is, they are recognized by naive observers as having a communicative function. Consequently, individuals may imitate meaningful novel actions differently from meaningless novel actions. Future experiments may wish to more directly assess the role of "meaning" in imitation independently of the familiarity of actions.

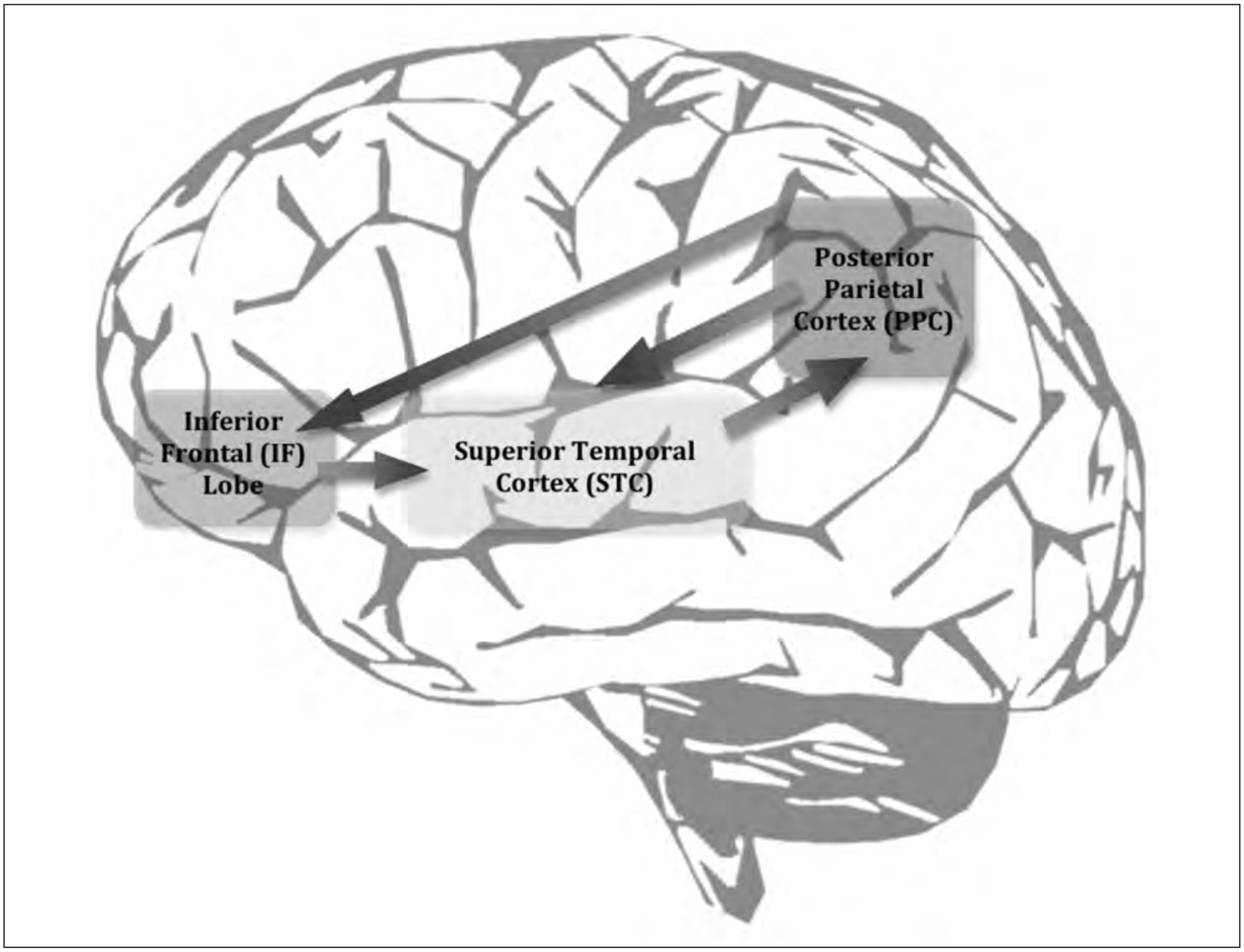

Figure 1. Familiar Motor Imitation Circuit. According to Carr et al. (2003) information flows as follows: (1) the STC codes early visual descriptions of actions and projects these representations to the PPC mirror neurons; (2) the PPC integrates representations of kinesthetic aspects of actions and projects this information to IF mirror neurons; (3) IF codes the outcome or the 'goal' of the target action; (4) IF and PPC send efferent copies of the action plan back to the STC, creating a matching 'resonance' mechanism between visual and motor representations of the same action event; (5) motor execution of imitation is initiated.

The results reported by Rumiati and Tessari as well as those by Shiffrar and Freyd make clear that different neural mechanisms mediate the imitation of novel as opposed to familiar responses. They further demonstrate that the distinction between familiar and novel imitation may best be characterized as a difference between recall and learning. In the case of familiar imitation, individuals recollect past (learned) experiences. Whereas in the case of novel imitation, individuals are encoding novel experiences and knowledge through observation or vicarious learning. In any event, these distinct imitation systems may feed into a more general motor imitation circuit such as that proposed by Carr and colleagues (2003) and summarized in Figure 1.

Additionally, neurobiological studies have demonstrated that observational learning—the core feature of novel imitation—has independent neurobiological circuits. Again, it must be stressed that in the multiple imitation framework, observational learning is not synonymous with imitation, particularly familiar imitation. There are two main differences between observational learning and novel imitation: First, novel imitation requires observational learning, but familiar imitation does not. Second, novel imitation requires observational learning in addition to copying. Observation learning requires only learning, not copying. The rationale here is that one may learn many things from observation (dispositional traits, the worth of things, what *not* to do or how not to behave) but we don't copy all we learn from others.

A number of lesion and single-cell recording studies suggest that observational learning is largely mediated by the right cerebellum. For example, Petrosini and colleagues (1999, 2000; 2007) demonstrated that rats tested in a Morris water maze task learn to locate a hidden platform in a pool one of two ways: by individual, trial-and error learning or by observing an experienced conspecific. To explore the cerebellum's role in this skill, Petrosini and colleagues removed the right hemicerebellum of naïve rats either after they had been given the opportu-

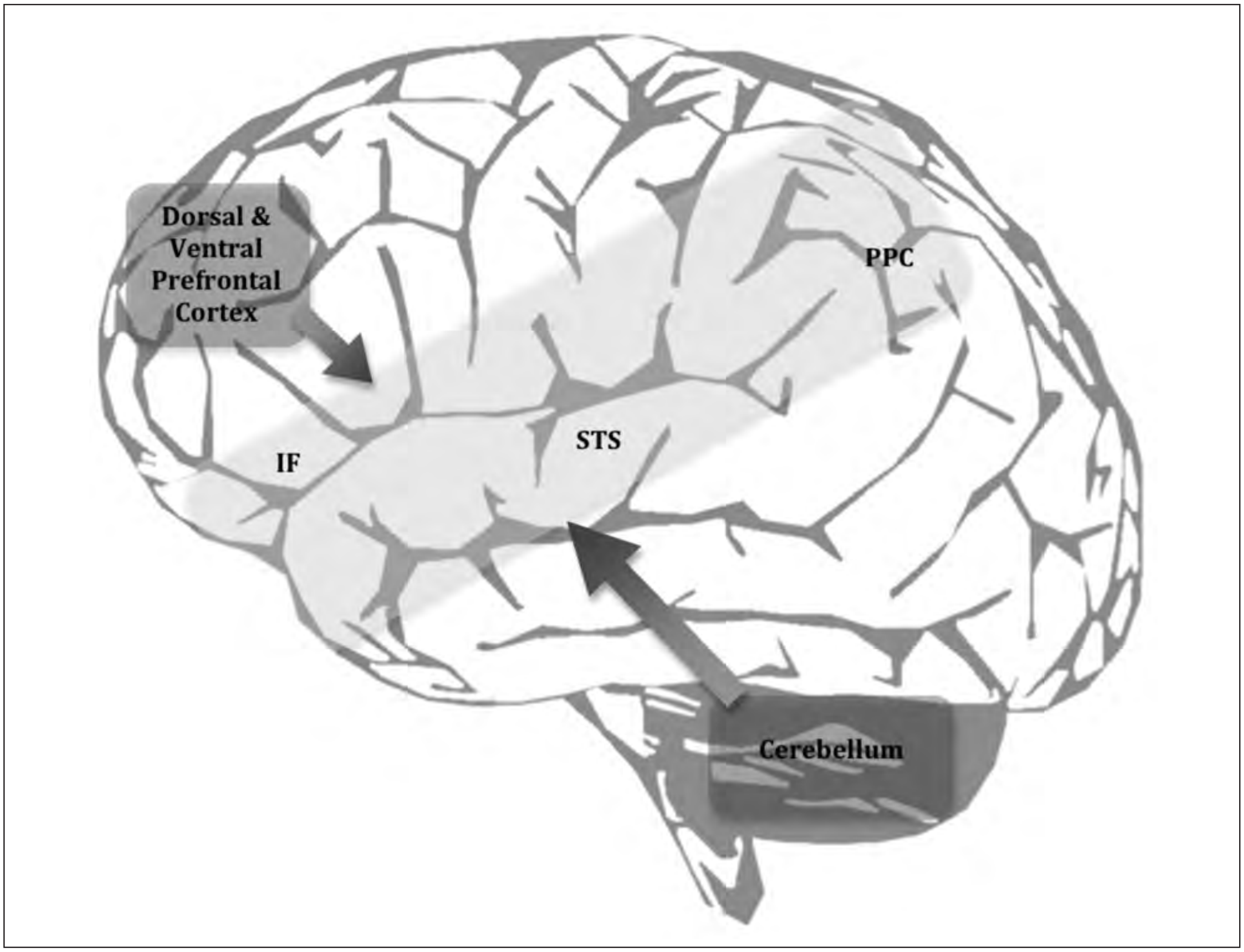

Figure 2. Novel Motor Imitation Circuit. A number of authors have pointed to the left posterior cerebellum as well as the dorsal and ventral prefrontal cortex as critical for (i) the intention to imitate (e.g., Chamindate et al. 2002) and (ii) observational learning (e.g., Petrosini, 2007). Leslie and colleagues (2003) have suggested that these cerebellar and frontal circuits that appear critical for novel motor imitation likely interact with circuits that appear responsible for familiar motor imitation (c.f., Figure 1).

nity to observe expert rats navigate through the pool and settle on a hidden platform (post-observation surgery treatment) or ablated the same part of the cerebellum before naïve subjects had been given the opportunity to observe the expert rat find the hidden platform (pre-observation surgery treatment). Results revealed that rats that received the post-observation surgery treatment learned how to find the hidden platform significantly faster than they would by trial and error. However, rats in the pre-observation surgery treatment failed to learn where the hidden platform was located. As a result, these rats performed randomly, eventually learning where the platform was located by trial-and-error learning.

Though these experiments do not exclude learning by perceptual/motivational mechanisms such as local enhancement, the results reported by Petrosini and colleagues (1999, 2000; 2007) have a number of significant implications. First, the removal of the right hemicerebellum in rats does not extinguish spatial or navigational abilities because all subjects are capable of learning where the hidden platform is located. Moreover, the ablation of this part of the cerebellum did not affect motor movements and/or coordination. Second, the difference between the performance of individuals in the pre- and post-observation surgery treatment demonstrates that the right cerebellum plays a significant role in learning. Third, the cerebellum's potential role in observational learning strongly suggests that a distinct circuit (independent of neural circuits mediating familiar imitation) is at work in social learning tasks in general and novel imitation in particular. This last point is corroborated by at least one other study with human subjects. Grèzes, Costes, and Decety (1998) showed that the left posterior cerebellum is uniquely active when subjects have the intent to imitate a novel response. Results demonstrated that the cerebellum becomes active when subjects are confronted with new rules that must be learned by observation (rather than by trial and error). In humans, as in rats, this cerebellar circuit (Grezes et al., 1998; Petrosini et al., 2000; 2007) appears to be independent of a separate frontal (e.g., BA 6, 9, 10, 46) and parietal (e.g., BA 40 & 7) circuit that have been linked specifically to familiar imitation (Carr et al., 2003; Rizzolatti et al, 2002). Nevertheless, while these cerebellar circuits appear to mediate observational learning, Leslie, Johnson-Frey and Grafton (2003), suggest that information from the left posterior cerebellum as well as the dorsolateral and ventral prefrontal cortex interact with the circuit (i.e., inferior frontal, STS and posterior parietal) associated with familiar motor imitation (Carr et al., 2003) in order to achieve novel motor imitation, for example (c.f., Figure 2).

Neurobiology of cognitive & motor imitation

Theoretically, the brain may imitate in one of two ways: either via a single imitation network involving hippocampal networks for familiar imitation (e.g., Rumiati et al., 2005) and a cortical-straital network for novel imitation or through distinct networks corresponding to the imitation of different types of stimuli such as motor, vocal, cognitive. At present the evidence is mixed. At least one imaging study on the "song system of the human brain" (Brown, Martinez, Hodges, Fox & Parson, 2004) suggests that familiar motor imitation and certain aspects of novel vocal imitation may have overlapping neural structures or be mediated by the same neural systems. While certain aspects of the human song system were unique, such as action in the superior part of the temporal pole (BA 38) others either overlap or are adjacent to the 'mirror neuron system' in the inferior frontal operculum (BA 44) that is known to play a critical role in familiar motor imitation (c.f., Figure 1). However, the overlap in the present study may have been due to sub-vocal rehearsal or the recall of lyrics from songs with a similar melody. Importantly, Brown et al. (2004) report that this system is only active when subjects are actively matching the pitch and rhythm of novel sequences but not when participants are recalling familiar melodies. Another neuroimaging study supports a dissociation between motor and cognitive imitation systems. Chaminade et al. (2002) presented subjects with a model executing one of three different aspects of an event: (a) the complete action arc from start to finish, (b) only the means used to achieve the action, and (c) only the result of the action. Subjects made one of three different responses: (a) passive observation, (b) imitated what was observed, or (c) acted freely. Because the task involved the intentional copying of actions, neural regions associated with higher-order motor representations and sensorimotor transformations in addition to the posterior Superior Temporal Sulcus (STS) were active across conditions. However, different neural regions were active when subjects observed and copied an entire event as opposed to when subjects observed and copied only the means or only the goals of that same event. Specifically, there was significant activation in the cerebellum (bilaterally) and the dorsolateral prefrontal cortex (DLPFC) when subjects copied both the means and the goals of an action. Yet, there was hypo- or no activation in these same regions when subjects copied the entire event. Moreover, despite the fact that some of the same regions were active when copying goals and means, regions of activation within DLPFC were not entirely overlapping. Furthermore, the medial prefrontal cortex was active only when subjects copied the means used to execute the action, whereas the left premotor cortex was active only when subjects copied the goals of the action. The fact that premotor cortex was differentially active in the course of copying goals versus means is of some significance as premotor cortex is associated with "mirror properties" in monkeys and humans (Buccino et al., 2001) and associated with the preparation and execution of goal-directed actions. Chaminade et al. (2002) argue that premotor cortex is only active when subjects copy goals because this is the only condition in which the means of the actions must be inferred from the observation event.

Taken together, these results suggest that the possibility for imitation-specific circuits that correspond to different imitation mechanisms. However, it cannot be overlooked that the studies by Chaminade et al. (2002) investigated goals, means, and action in the context of a motor imitation task rather than a task that involved copying non-motor or cognitive rules (independently of the execution of specific motor actions) as was done by Subiaul and colleagues (2004; 2007), for example. Moreover, this study did not distinguish between copying familiar (familiar imitation) versus unfamiliar (novel imitation) goals and means. So, for example, the system that mediates the copying of novel goals may differ from the system that mediates the copying of familiar goals.

MOSAIC IMITATION SKILLS IN APES

The comparative study of imitation: Apes and humans

Certainly, social learning is common in the animal kingdom (Zentall, 2007) and sophisticated local traditions exist in apes (Whiten et al., 1999; van Schaik et al., 2003) and to a lesser degree in monkeys (Panger et al., 2002; Perry et al., 2003). And, as can be seen in Table 1, while there are a number of similarities between human and nonhuman 'cultures' only humans have cultures that build on prior knowledge and accumulate over time (Boyd & Richerson, 1985; Henrich & McElreath, 2003; Subiaul, 2007; Tomasello, 1999; Tomasello, Kruger & Ratner, 1993). Given our species' penchant for cultural learning and the extent to which our survival depends on that learning, there is perhaps no greater question than what underlies such skills. One (arguably) uniquely human skill is the ability to copy a broad range of rules—motor, vocal, cognitive—from a model. Might differences in cultural learning be explained in part by differences in what and how apes and humans imitate?

Table 1. Features of 'Culture.' Below is a list of the characteristics of culture proposed by different authors and their distribution in humans, non-human (NH) apes and monkeys (specifically, capuchin monkeys). The table demonstrates that apes share many features in common and differ from monkeys.

Components of Culture	Humans	NH Apes	Monkeys
Innovation: New behavioral pattern is invented*	+	+	+
Dissemination: Transmitted from individual to individual*	+	+	+
Durability: Pattern persists beyond demonstrator's presence*	+	+	–
Diffusion: Pattern spreads across groups*	+	+	+
Tradition: Pattern endures across generations*	+	+	–
Standardization: Pattern is consistent and stylized*	+	+	~
Species-Valid: Not an artifact of human influence*	+	+	+
Transcendent: Not determined by biophysical environment*	+	+	+
Accumulation: Traditions build over time**	+	–	–
Imitation: Ability to copy novel motor responses‡	+	+	–
Variability: Two or more patterned behaviors in more than one domain§	+	+	+

**Criteria from Krober (1928), ** Tomasello & Call (1997), ‡Galef (1992), Whiten & van Schaik§ (2007), + (present), – (absent), ~ unknown or debatable*

As with the attribution of mental states, there has been a long-lasting controversy over whether or not humans are unique in the ability to learn from others. In fact, Aristotle argued in the *Poetics* that humans are "the most imitative creatures in the world and learn first by imitation." In the past 30 years, interest in imitation learning has experienced a renaissance, particularly as scientists have found that from birth neonate copy the facial expressions of adults (Meltzoff and Moore, 1977) and primatologists have documented various instances of tool traditions in populations of wild chimpanzees (McGrew, 1992; 1994; 2001; Whiten et al., 1999) and orangutans (van Schaik et al., 2003). However, to date only eleven studies have directly compared imitation learning in human and non-human [adult] apes using analogous procedures (Call, Carpenter, Tomasello, 2005; Call and Tomasello, 1995; Herrmann et al., 2007; Horner and Whiten, 2004; 2005; 2007; Horner, Whiten, Flynn & deWaal, 2006; Horowitz, 2003; Nagell et al., 1993; Tomasello, Savage-Rumbaugh, and Kruger, 1993; Whiten, Custance, Gomez et al., 1996). Six of these studies have reported that on an operational task, where a tool or object had to be manipulated in a certain manner to achieve a specific result (or reward), humans reproduce the demonstrator's actions with greater fidelity (i.e., imitation) than did mother-reared apes (Call, Carpenter and Tomasello, 2005; Herrmann et al., 2007; Horner & Whiten, 2007; Call and Tomasello, 1995; Nagel, et al., 1993; Tomasello et al., 1993). The other studies reported both similarities and differences between humans and peer-reared apes when executing specific actions on an object following a demonstration (Horner and Whiten, 2004; 2005; Horner et al., 2006; Whiten et al., 1996). And one, found no differences between the performance of adult humans and other apes (Horowitz, 2003).

Comparing familiar vs. novel motor imitation in primates

Given these results, it is obvious that there's no simple answer to the question, 'Do apes, ape?' How might one explain these seemingly conflicting reports of similarities and differences, particularly if imitation is viewed as one unitary faculty that animals either have or lack entirely? One possibility is that these different studies are measuring different imitation mechanisms. When viewed this way it appears that apes and humans share some imitation mechanisms (hence the similarities in some studies) but do not share all (explaining some of the differences). Using the multiple imitation framework outlined above, studies such as, Horner & Whiten (2004; 2005) and Horner and colleagues (2006) are likely to be tasks of familiar motor imitation, whereas studies such as Horner & Whiten (2007) are tasks of novel motor imitation. Without question, novel motor imitation tasks are harder than familiar motor imitation tasks. What makes novel motor imitation harder is that to be successful the subject must first attend to the relevant information (hand or body part, tool or object), create a new action representation and then match this abstract motor representation with a new action plan. The same is not true for familiar imitation tasks because the observation of a familiar action likely primes that same action in memory (i.e., recognition memory). In this case, the construction of a novel action plan is not necessary as it is recalled from memory.

There are likely to be other differences that contribute to differences in motor imitation performance among apes. Perhaps the most significant has to do with toolknowledge and tool-use. Most studies that require animals to use tools in ways that they do not do naturally in the wild tend to find differences between human and non-human subjects (e.g., Herrmann et al., 2007; Horner & Whiten, 2007). When the imitation task involves using tools in ways that are more 'naturalistic' (i.e., behaviors that typically appear in the wild such as probing with a stick or pushing objects out of the way), more similarities are reported between humans and other apes (e.g., Horner et al., 2006; Hopper et al., 2008). However, there are some studies where apes are required to execute 'familiar' actions—such as pulling or pushing—on unfamiliar objects or in novel experimental circumstances (Call & Tomasello, 1995; Herrmann et al., 2007). These studies, too, tend to report more differences than similarities between humans and other apes. Johnson-Frey (2003; 2004) and Povinelli (2000) have suggested that there may be in some cases subtle and in other cases dramatic differences between humans and other animal's orientation to objects with tool properties. For instances, some of the differences in imitation performance may be due to differences in the "Grasp" and "Manipulation" motor system that are mediated, in part, by circuits in the parietal and frontal lobe. While Johnson-Frey suggests that differences in these two motor systems may be negligible, how these systems interact with conceptual systems mediating causal action likely produces significant species differences, as borne out by a number of comparative studies on chimpanzee tool-use (e.g., Povinelli, 2000). Novel motor imitation likely depends on input from these various systems, without which it cannot operate. The same is likely to be less true for familiar motor imitation, as experience allows individuals to recall existing motor representations and rehearsed motor action plans.

There is some support for the hypothesis that chimpanzees differentially imitate novel versus familiar actions (Myowa-Yamakoshi et al., 1999). Myowa-Yamakoshi and colleagues presented chimpanzees with a number object-based actions that they characterized as general actions (familiar actions on objects that were commonly observed) and non-general actions (relatively novel actions on objects that were not commonly observed). This corresponds roughly to the proposed distinction of familiar versus novel imitation. They applied this scheme to different actions on objects that ranged from copying single but specific actions on objects such as banging the bottom of a bowl, to copying actions that involve directing objects to specific body parts such as putting the bowl on the head, to copying object-object interactions such as putting a ball in a bowl. Results revealed that performance was best for familiar actions and relatively poor for novel actions. Chimpanzees in these studies performed best in the object-object condition and worst in the single-action condition. However, these results are derived from multiple trials and do not represent first trial performance. Unfortunately, no data is presented on 'familiar' versus 'novel' actions in these different conditions. But, Myowa-Yamakoshi and colleagues note that chimpanzees rarely copied any type of action (familiar or novel) on the very first trial. A strong indication that all or any subsequent copying behavior was likely mediated by familiar rather than motor imitation. Yet, given the hypotheses of the multiple imitation framework it's surprising that object-object actions were ultimately easier to reproduce than single actions on objects. There may be two explanations for this result. One possibility is that the objects used in the study constrained or limited the range of object-object responses as compared with the single action on object condition, where many more responses were possible. So, for instance, the object-object action most accurately copied by chimpanzees was the familiar action of putting a ball in a bowl; an object-object interaction with clear causal affordances. Given that the chimpanzees tested in these studies have a lot of experience putting things in bowls, the fact that this action was copied with the highest fidelity shouldn't be surprising even when compared to a relatively simple but arbitrary (and, perhaps, novel) single action like rubbing the bottom of the bowl. A second explanation may have had to do with the fact that when subjects failed to reproduce the action, they received explicit instruction. During the 'Teaching Phase' the demonstrator trained the subject to produce the target action through "verbal and gestural guidance, molding, shaping with verbal praise and food reinforcements, or a combination of these methods" (Myowa-Yamakoshi et al., 1999: 130). One or both of these explanations may explain the difference reported between copying a single action on objects and copying object-object actions.

Recently, a number of studies have focused on a special type of familiar imitation: oral facial imitation. Comparative developmental psychologists have shown no significant differences between a human and a chimpanzee infant's ability to copy the oral-facial expressions of a model. Chimpanzees, like human infants (e.g., Meltzoff and Moore, 1977), reproduce tongue protrusions, lip protrusions, and mouth openings in response to a model displaying the same expression (Myowa-Yamakoshi, Tomonaga, Tanaka, and Matsuzawa, 2004). There are also parallels in the developmental trajectory of oral-facial imitation in both of these species. Myowa-Yamakoshi and colleagues report that after 9 weeks of age, the incidence of oral-facial imitation in chimpanzees slowly disappears. A similar phenomenon has been reported for human infants (Abravanel and Sigafoos, 1984). In short this study found no qualitative differences between human infants and infant chimpanzees in oral-facial imitation. Recently, Ferrari and colleagues (2006) have reported oral-facial imitation in infant rhesus macaques. However, researchers have cast doubt on the notion that matching oral-facial responses is best characterized as imitation (as defined here or elsewhere). First, an extensive review of the literature revealed that only tongue protrusions are matched by human infants (Anisfeld, 1991; 1996; Anisfeld et al., 2001). Second, and perhaps most surprisingly, a number of studies have demonstrated that a moving pen (Jacobson, 1979), blinking light(s) (Jones, 1996) and music (Jones, 2006) are all as likely to elicit tongue protrusions in neonates as is watching a model display the same behavior. However, the study by Ferrari and colleagues on neonatal imitation in macaques is unique in that the experimental design included non-social controls such a spinning disk in addition to the typical social stimuli in such experiments (i.e., mouth opening, tongue protrusions, etc.). Ferrari and colleagues reported that lipsmacking and tongue protrusions occurred significantly more often in response to displays of those same actions than they did to other types of stimuli. However, lipsmacking occurred the most often in response to different types of stimuli, much like tongue protrusions in human infants (Jones, 1996). Ferrari et al. (2006) noting the amount of inter-individual variation and the sensitivity to specific oral-facial movements (e.g., mouth openings and tongue protrusions) in both human and monkey neonatal imitation pointedly caution that "the capacity to respond to the model may not reflect a general imitative skill but rather a sensorimotor sensitivity tuned to specific facial gestures" (p. 1506). At this point it is impossible to say with any certainty whether these results are mediated by a mechanism independent of the imitation faculty.

Taken together, the research reviewed above suggests that the motor imitation skills of primates are a mosaic of many different imitation mechanisms mediating the copying of different types of responses and likely represent adaptive solutions to specific problems. From this it follows that paradigms that conceptualize imitation as one unitary faculty that an individual either has or lacks entirely is problematic. As has been already noted, humans and other primates appear to share some imitation mechanism such as the ability to copy familiar motor actions and even novel cognitive rules (Subiaul, 2007; Subiaul et al., 2004; 2007) explaining the similarities reported by some comparative researchers. However, it's also clear that apes do not possess all the imitation mechanisms of a human 2.5 year old. This conclusion appears to be particularly true for novel motor imitation, a mechanisms that may rely on many higherlevel conceptual mechanisms. The fact that humans possess more imitation mechanisms sensitive to different types of stimuli, rather than a domain- and contentgeneral imitation mechanism, explains our species ability to copy a broad range of behaviors and responses relative to other primates.

THE EVOLUTION OF THE IMITATION FACULTY

Ecological & technological selection

Any contemplation of the mosaic evolution of the imitation faculty must begin with the question 'What are these different imitation mechanisms for?' How might having a simple imitation faculty consisting of only familiar imitation, for example, be adaptive? How might it increase fitness? Familiar imitation likely solves the problem of where and when to execute species-typical behaviors in appropriate contexts as well as coordinate/affiliative activies. In contrast, novel imitation solves the problems of acquiring information at a low cost. In both cases, imitation reduces the costs (e.g., time, energy) associated with trial-and-error learning. So whereas familiar imitation minimizes the need to learn *where* or *when* to execute familiar responses, in the case of novel motor imitation, it minimizes learning *how* and, perhaps *why* to do a novel action.

As many have noted, these problems are particularly acute in environments that are constantly changing. That environment may be social, it may be physical or it may be both. The more flux, the greater the need to quickly adapt to the new situation and the greater the selection pressures favoring various imitation mechanisms. This view has been supported by mathematical models that have, in effect, demonstrated that the evolution of the imitation faculty is linked to life in ever-changing environments (Boyd & Richardson, 1986; Henrich & McElreath, 2003). An evaluation of animals such as birds and primates who live in variable social and physical environments, suggests that these animals possess social learning skills consistent with at least a basic imitation faculty (Reader & Laland, 2002; Lefebvre et al., 1998). Interestingly, Reader and Laland (2002) have reported that among primates, brain size correlates most significantly with social learning, but also with individual learning ('innovation') and tool-use. In their analysis, social learning, individual learning and tool use are all strongly inter-correlated (Reader & Laland, 2002). Similar data exists for birds (Lefebvre, et al. 1996; Lefebvre, et al., 1998), providing evidence of convergent evolutionary processes.

The above evidence indicates that novel motor imitation is likely to be a derived feature and a characteristic of the hominoid imitation faculty; one that is perhaps intricately linked with tool-use. In this view, the more dependent an organism is on technology or motor learning for subsistence, the more imitation mechanism that animal is likely to possess (Figure 3). The main reason being that the use of technology—tools— requires specialized sensorimotor and inferential mechanisms working in a coordinated fashion to selectively attend to and encode certain types of information that produces a template that serves as the basis for a matching response. Such pressures should be stronger among apes than

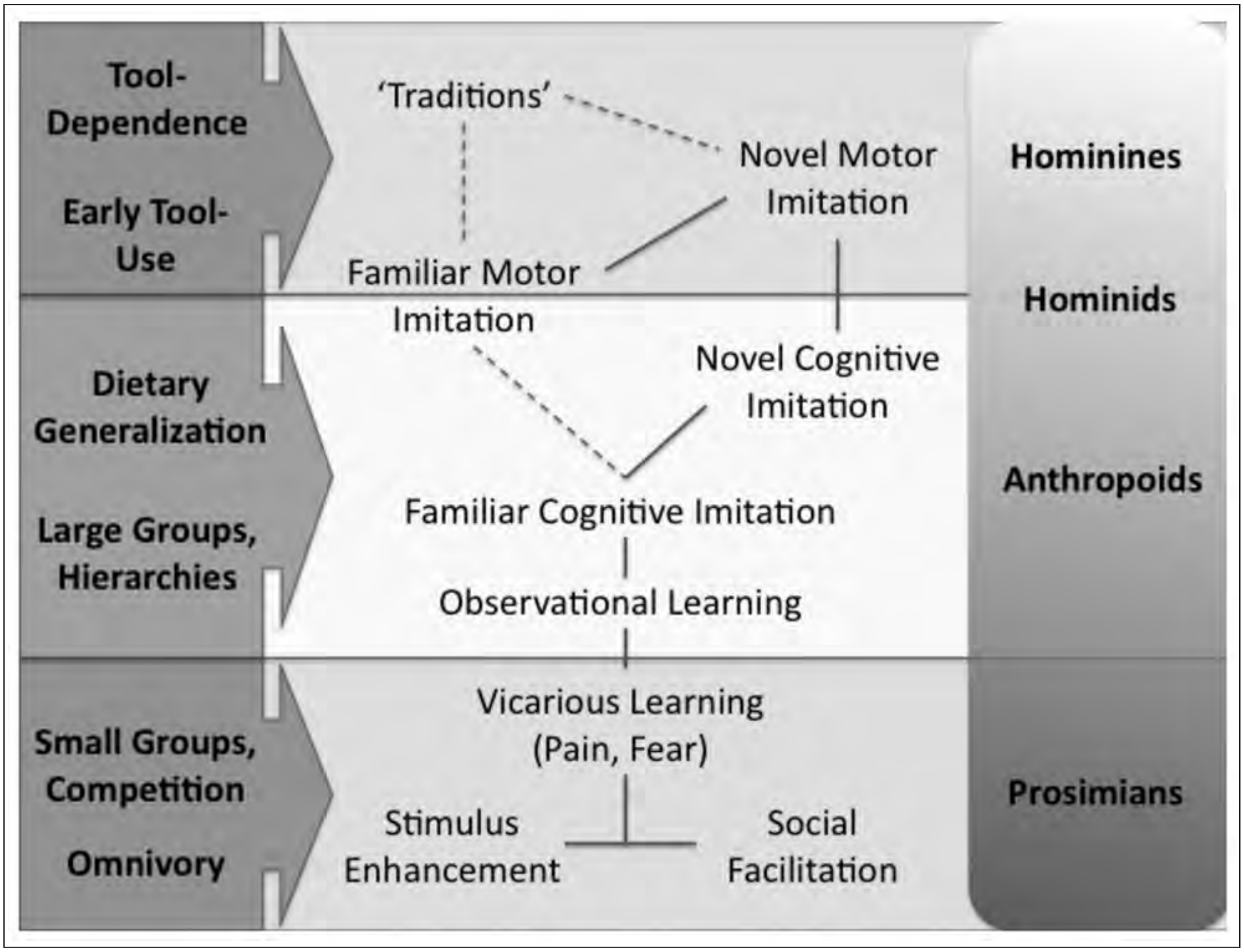

Figure 3. Mosaic Evolution of Imitation. The imitation faculty likely evolved from primitive circuits mediating vicarious learning; specifically, the vicarious learning of fear, disgust and pain. The diagram presents a simplified summary of how certain selective forces and ecological problems may have acted upon these primitive circuits and produced a variety of distinct imitation mechanisms in different primate groups.

monkeys because while monkeys have specialized dentition and digestive systems, apes have somewhat generalized dental anatomy and, with the exception of gorillas, lack specialized digestive systems (Ankel-Simons, 2000). These anatomical differences mean that whereas monkeys are able to enjoy a relatively diverse diet, apes don't have the same luxury. In monkeys, diets range from non-ripe fruits and mature leaves to insects, small animals and gum. Ape anatomy, however, limits dietary options to a narrow range of foods that consist mostly of mature, nonfibrous fruits with high sugar and calorie content (Maier, 1984). As a consequence of these dietary limitations, the great apes occupy a fairly narrow range of ecological habitats, being largely restricted to tropical and woodland forests (Potts, 1998; 2004). Contrast the narrow ecological range of chimpanzees and orangutans to that of macaques that have made a home in the arid lands of Africa as well as the snowy hillside of Japan.

These ecological, morphological and dietary pressures that, among primates, are mostly unique to the great apes, placed a premium on novel behavioral, cognitive, and life history strategies that are critical to fitness (Potts, 2004) and presumably served as a compensatory mechanism for morphological limitations. One such behavioral strategy used to broaden the apes diet is the systematic pursuit of prey in groups—or 'hunting'—(Watts & Mitani, 2002), another has been extractive foraging using tools (Goodall, 1986; Whiten et al., 1999). Yet another, might have been the fission-fussion social organization of chimpanzees and bonobos. Holloway (1967; 1981; 1996) argued that these variables were likely to be "prime interactive agents in human brain evolution" (Holloway, 1996: 97). But I proposed that these behavioral and sociological innovations—hunting, fission-fusion, and tool-use—likely favored an elaboration of the imitation faculty, in particular, the evolution of a robust novel imitation mechanism that was functionally integrated with other domain-specific imitation mechanisms (e.g., motor and cognitive imitation) and by extension shaped neural organization and evolution. Certainly, the novel motor imitation skills of apes are less robust than those known to be present in children as young as 2.5

years of age (Herrmann et al., 2007). These more derived novel motor imitation skills likely date to the first members of the genus *Homo*, where the need and dependence on stone-tool technology and other methods of subsistence including hunting and gathering placed increasing pressures on various mechanisms of the imitation faculty. Some of these elaborations may have included functional connections with other conceptual systems mediating Theory of Mind and causality but also affective systems mediating cooperation and empathy.

Nevertheless, given the ecological circumstances of non-human great apes, an imitation faculty capable of novel motor imitation would immediately increase the fitness of chimpanzees, for example, as it would have provided individuals with the skills to effectively steal the technical knowledge of conspecifics and immediately use that knowledge to supplement their diets. Given the importance of such a skill, it should then be no surprise that apes have elaborate tool-traditions which afford the means to develop and maintain these skills necessary for sustenance (Whiten et al., 1999). Yet, note that traditions as they exist in chimpanzees and orangutans are mostly absent in monkeys (c.f., Table 1). And where they exist, as appears to be the case in capuchin monkeys, they comprise of just 2 or 3 behaviors which lack the diversity and complexity that characterized chimpanzee and orangutan behavioral traditions (Boinski et al., 2003; Panger et al., 2002; Perry et al., 2003). These differences may rest on the fact, in captivity, among chimpanzees such traditions are mediated by motor imitation coupled by a strong tendency to always use the group's preferred technique (see Whiten, 2005 for a review). No comparable evidence exists for capuchin monkeys, or any other monkey species. Perhaps the discontinuity between traditions in monkeys and apes is not surprising, given that monkeys', as a group, are characterized by numerous anatomical specializations that are specifically adapted to their niche, which in no small measure grants them the ability to exploit a wide range of diets and habitats without tools or the need for sophisticated traditions.

Imitation-Brain Co-Evolution

Given the evidence that capuchin, marmoset and rhesus monkeys as well as chimpanzees, orangutans and gorillas share a familiar imitation mechanism, familiar imitation is likely to be the most basic and ancestral feature of the imitation faculty, and the feature that is likely to be present in all animals that possess a faculty of imitation. The models proposed by Boyd & Richardson (1986) and Henrich & McElreath (2003) explain this facet of the imitation faculty best. While it's possible for an animal to possess an imitation faculty that can copy only familiar responses (familiar imitation), it's difficult to imagine an imitation faculty capable of novel imitation, yet incapable of familiar imitation. From this it follows that the evolution of a derived imitation faculty that includes the ability to copy novel responses is premised on mechanisms the mediate familiar imitation. Some of the neurobiological evidence reviewed above provides some insights into how the elaboration of the STS-F5-PS circuit in the macaque brain (c.f., Figure 1), for example, can make at least novel motor imitation possible via the representation of intransitive actions (Rizzolatti, 2005) and input from other neural regions, in particular dorsolater and vertal prefrontal cortex as well the posterior cerebellum (c.f., Figure 2). However, logically, novel motor imitation is premised on novel cognitive imitation. The former seems difficult (if not impossible) without first having the ability to copy novel cognitive rules. But what selection pressures might have driven the elaboration of this faculty? One possibility is the need to develop and acquire more effective extractive foraging techniques; specifically, techniques that require the use of tools. Such selection pressures on observable behaviors certainly affected neural organization and perhaps contributed to mosaic brain evolution (Holloway, 1967; 1996). Perhaps it's no surprise that the regions that Holloway and colleagues have identified as early candidates of reorganization such as parietal, cerebellar and striate cortex, also happen to be areas critical for imitation (c.f., Figures 1 and 2).

Specifically, the evolution of the imitation faculty most certainly involved structural and organizational changes to a number of domain-general and domain-specific neurocognitive circuits: including attentional networks necessary to focus attention on relevant information, memory systems for the purpose of representing, encoding and recalling the target information, as well as changes to the 'reward' and 'empathic' systems, necessary for learning and vicarious reinforcement. For instance, observational learning likely resulted from changes to the 'reward networks' of the brain. Specifically, changes to the left anterior insula, associated with the facial recognition as well as the imitation of 'disgust' (Carr et al., 2003) and along with the anterior cingular cortex, mediating pain empathy (Singer et al., 2004), are most certainly involved in vicarious punishment (c.f., Bandura, 1977). These changes provided individuals with a powerful tool, the power to learn what not to do or what behaviors are most likely to decrease fitness. Such vicariously learned aversions have been reported in many animals including birds, rats and primates (for review see: Olsson & Phelps, 2007). But there must also have been changes to structures that contribute to vicarious positive reinforcement. That is, a mechanisms that promotes fitness-increasing behaviors but through vicarious rather than direct learning. Unfortunately, there's very little to nothing that has been done about vicarious positive reinforcement or the study of positive empathy. A better understanding of the role of the vicarious experience of positive emotions will go a long way to explain vicariously learning; a central component of novel imitation and by extension how pressure to make individuals better novel imitators directed brain evolution and re-organization.

CONCLUSIONS

The data summarized above provides compelling evidence that the imitation faculty is mosaic and given its distribution among primates, its evolution and neural organization appears to reflect this fact. Holloway and colleagues have identified a number of neural regions such as cerebellar and parietal cortex that have undergone significant organizational changes. Others, such as Deacon (1997) and Semendeferi et al (2001), have argued for relative expansions of prefrontal regions (see Holloway, 2002 for a critique), structures that have been implied in both familiar and novel imitation. Given our knowledge of tool traditions in contemporary chimpanzee societies and evidence from the cognitive neurosciences identifying frontal, parietal, and cerebellar regions as critical for imitation, it might not be so surprising that these neural regions, central to imitation, appear to have undergone radical changes in the course of human brain evolution.

The mosaic nature of the imitation faculty, consisting of the ability to copy different types of rules and responses including, familiar motor actions (i.e., familiar motor imitation) as well as novel cognitive rules (i.e., novel cognitive imitation), most certainly afforded monkeys the ability to appropriately copy the (familiar) actions of their conspecifics. The evolution of this skill was likely to be a specific adaptation to the pressures of group living, such as pressures associated with managing social hierarchies and group feeding. From this it follows that familiar imitation should be common in most social species where the ability to adaptively copy the familiar behaviors of conspecifics during synchronized activities like foraging, feeding and territory defense would afford important fitness benefits; reviews of social learning in a variety of animals suggests that this is the case (see Zentall, 2006). These cognitive mechanisms mediating familiar motor imitation and novel cognitive imitation as well as observational learning provided the biological raw materials for the evolution of novel motor imitation. Here it's proposed that a combination of sociological, ecological and technological variables favored such a skill. From this it follows that novel imitation should be common in species with generalized anatomies and where technical (or specialized motor) knowledge is critical for survival. Thus, in this view, the elaboration of a critical social cognition skill—imitation—was the product not simply of social factors but physical factors associated with knowledge of tools, motor actions and spatial relations.

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